

RESEARCH ARTICLE

First records of aneuretine ants (Hymenoptera: Formicidae: Aneuretinae) in late Eocene Rovno amber (Ukraine)

Alexander Radchenko¹, Mykola Khomych²

¹ Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine, 15, B. Khmel'nitskogo str., Kyiv-30, 01030, Ukraine

² Village Voronky, Volodymyrets Distr., Rivne Prov., 34330, Ukraine

Corresponding author: Alexander Radchenko (agradchenko@hotmail.com)

Received 11 April 2022 | Accepted 23 July 2022 | Published 31 December 2022

Citation: Radchenko A, Khomych M (2022) First records of aneuretine ants (Hymenoptera: Formicidae: Aneuretinae) in late Eocene Rovno amber (Ukraine). Travaux du Muséum National d'Histoire Naturelle "Grigore Antipa" 65(2): 69–80. <https://doi.org/10.3897/travaux.63.e85206>

Abstract

Aneuretinae is an enigmatic ant subfamily with poorly defined morphological boundaries. *Aneuretus simoni* Emery, 1893, found only in Sri Lanka, is a "living fossil", the only known extant species of Aneuretinae. In the distant past, however, Aneuretinae was more diverse and widespread, including eight extinct genera spread across North America, Europe, and the Russian Far East. Here, we report two fossil Aneuretinae species, *Protaneuretus succineus* Wheeler, 1915 and *Paraneuretus tornquisti* Wheeler, 1915, found in late Eocene (Priabonian, 37.8–33.9 Ma) Rovno amber (Ukraine), providing distinguishing morphological features and measurements. These species, the first recorded Aneuretinae in Rovno amber, were originally described from Baltic amber of similar Priabonian age. These new records raise the number of reported ants in Rovno amber to 77 species from 39 genera and 9 subfamilies, and indicate that in the late Eocene Aneuretinae were distributed both on the northern and southern coasts of the Paratethys. Fossil evidence suggests that Aneuretinae originated in the Northern Hemisphere and only entered India and Sri Lanka after the Indian subcontinent collided with Asia ~59 Ma. Why Aneuretinae survived to the present only in Sri Lanka remains a mystery.

Keywords

Fossils, morphology, paleontology, *Paraneuretus tornquisti*, *Protaneuretus succineus*, taxonomy.

Introduction

Aneuretinae is an enigmatic ant subfamily with poorly defined morphological boundaries. Emery (1893) described the ant species *Aneuretus simoni* from Sri Lanka, placing it in its own monotypic genus. Emery (1913) established the tribe Aneuretini, within the subfamily Dolichoderinae, for this one genus. Clark (1951) proposed his own classification system of ants at the subfamily level. In doing so, he emphasized that did not personally study representatives of the genus *Aneuretus*, but its difference from other ants allows him to raised Aneuretini to subfamily rank, the Aneuretinae. Wilson et al. (1956) rediscovered populations of *A. simoni*, described queens and males, and confirmed the status of Aneuretinae. *Aneuretus simoni*, found only in Sri Lanka, is a “living fossil”, the only known extant member of the ant subfamily Aneuretinae.

In the distant past, however, Aneuretinae was more diverse and widespread. In addition to *A. simoni*, Aneuretinae currently includes twelve described species in eight extinct genera (*Aneuretellus* Dlussky, 1988, *Britaneuretus* Dlussky et Perfilieva, 2014, *Cananeuretus* Engel et Grimaldi, 2005, *Mianeuretus* Carpenter, 1930, *Napakimyrma* LaPolla et Barden, 2018, *Paraneuretus* Wheeler, 1915, *Pityomyrmex* Wheeler, 1915 and *Protaneuretus* Wheeler, 1915), found in North America, Europe, and the Russian Far East, and ranging in age from the Cretaceous (Campanian, 83.6–71.2 Ma) to the latest Eocene (~35–34 Ma) (Cockerell 1915; Wheeler 1915; Carpenter 1930; Dlussky 1988; Dlussky and Rasnitsyn 2003; Engel and Grimaldi 2005; Dlussky and Rasnitsyn 2009; Dlussky and Perfilieva 2014; Dlussky et al. 2015; LaPolla and Barden 2018; Dubovikoff et al. 2020). Dlussky (1996) established the monotypic genus *Burmomyrma* based on a poorly preserved, headless specimen from Burmese amber (Myanmar, late Cretaceous, early Cenomanian, ~100 Ma) and proposed it may belong to Aneuretinae. However, Lucena and Melo (2018) excluded this genus from Formicidae and suggested that it most likely belongs to the family Falsiformicidae Rasnitsyn, 1975, but Boudinot et al. (2022) treated *Bormomyrma incertae sedis* in Formicidae.

In the course of our ongoing investigations of ants in Rovno amber (Priabonian, 37.8–33.9 Ma) from Rivne Oblast (province), Ukraine, we encountered two worker specimens we identified as Aneuretinae, a subfamily previously unknown from this amber. Rovno amber, named after the city of Rivne (formerly Rovno), is found in the Rivne Oblast, Ukraine and nearby areas of Ukraine and Belarus. To date, 75 ant species from 37 genera have been recorded from Rovno amber (Dlussky and Rasnitsyn 2009; Perkovsky 2016; Radchenko and Dlussky 2016, 2018a, 2018b, 2019; Radchenko et al. 2018; Radchenko and Perkovsky 2018, 2020; Radchenko and Khomych 2020; Radchenko 2020, 2021; Radchenko et al. 2021; Radchenko and Proshchalykin 2021).

Material and methods

In the present study, we examined two ant worker specimens embedded in two pieces of Rovno amber from Rivne Oblast, Ukraine: one from the Volodymerets district, which we identified as *Protaneuretus succineus* Wheeler, 1915, and the other from Klesov, Sarny district, which we identified as *Paraneuretus tornquisti* Wheeler, 1915. The *P. succineus* worker is an intact, perfectly preserved specimen, and *P. tornquisti* is fairly well-preserved specimen, but with the right side and part of the dorsum of the body partially covered with an opaque film. The *P. succineus* specimen is deposited in the collection of M. Khomych (collection number F-200), and the *P. tornquisti* specimen is deposited in the I. I. Schmalhausen Institute of Zoology of NAS of Ukraine, Kiev (SIZK) (collection number K-9135).

We photographed the ant specimens using a Leica Z16 APO stereomicroscope equipped with a Leica DFC 450 camera and processed with the LAS Core software. We measured the specimens using a Leica MZ6 stereomicroscope with an ocular-micrometer at a maximum magnification x100. Not all features of the examined specimens were properly visible and measurable, so only clearly visible details (calculated with a precision of 0.01 mm) were measured.

Measurements included: **HL** – maximum length of the head in dorsal view, measured in a straight line from the anteriormost point of clypeus to the mid-point of occipital margin; **SL** – maximum length of the scape measured in a straight line from its apex to the articulation with condylar bulb; **OL-1** – maximal diameter of the eye; **OL-2** – minimal diameter of the eye; **MsL** – length of the malar space, measured from the anterior margin of the eyes to the articulation with the mandible; **MdL** – length of the mandible from the tip of apical tooth to the outer point of insertion with the head; **ML** – diagonal length of the mesosoma seen in profile from the anterior margin of neck shield to the posterior margin of propodeal lobes; **MH** – height of the mesosoma, measured from the upper level of promesonotum perpendicularly to the level of lower margin of mesopleuron; **PL** – maximum length of the petiole, measured from the posterodorsal margin of the petiole to the articulation with the propodeum; **PH** – maximum height of the petiole in profile, measured from the uppermost point of the petiolar node perpendicularly to the lowest point of the petiole; **HTL** – maximum length of the metatibia; **HFL** – maximum length of the hind femur; **fun1L**, **fun2L** – length of the first and second funicular segments, respectively. **TL** – total length was calculated as the sum of HL + ML + PL + length of the gaster. Indices included: $SI=SL/HL$, $OI-1=OL-1/HL$, $OI-2=OL-1/OL-2$, $MsI= MsL/OL-1$, $MdI= MdL/HL$, $PI-1=PL/PH$, $PI-2= PL/HL$, $MI=ML/MH$, $funI=fun2L/fun1L$.

Results

We identified the two specimens as *Protaneuretus succineus* Wheeler, 1915 and *Paraneuretus tornquisti* Wheeler, 1915, species originally described from Baltic amber

of similar Priabonian age. We found that Wheeler's (1915) descriptions and drawings of *Protaneuretus succineus* and *Paraneuretus tornquisti* are accurate and exhaustive. The workers and queens of these genera are well distinguished from those of the subfamilies Formicinae and Dolichoderinae found in late Eocene European ambers primarily by the presence of a sting, as well as the shape of the petiole, which has a rather long anterior peduncle combined with high thick scale (Figs 1, 2; see also Wheeler 1915, figs 31, 32).

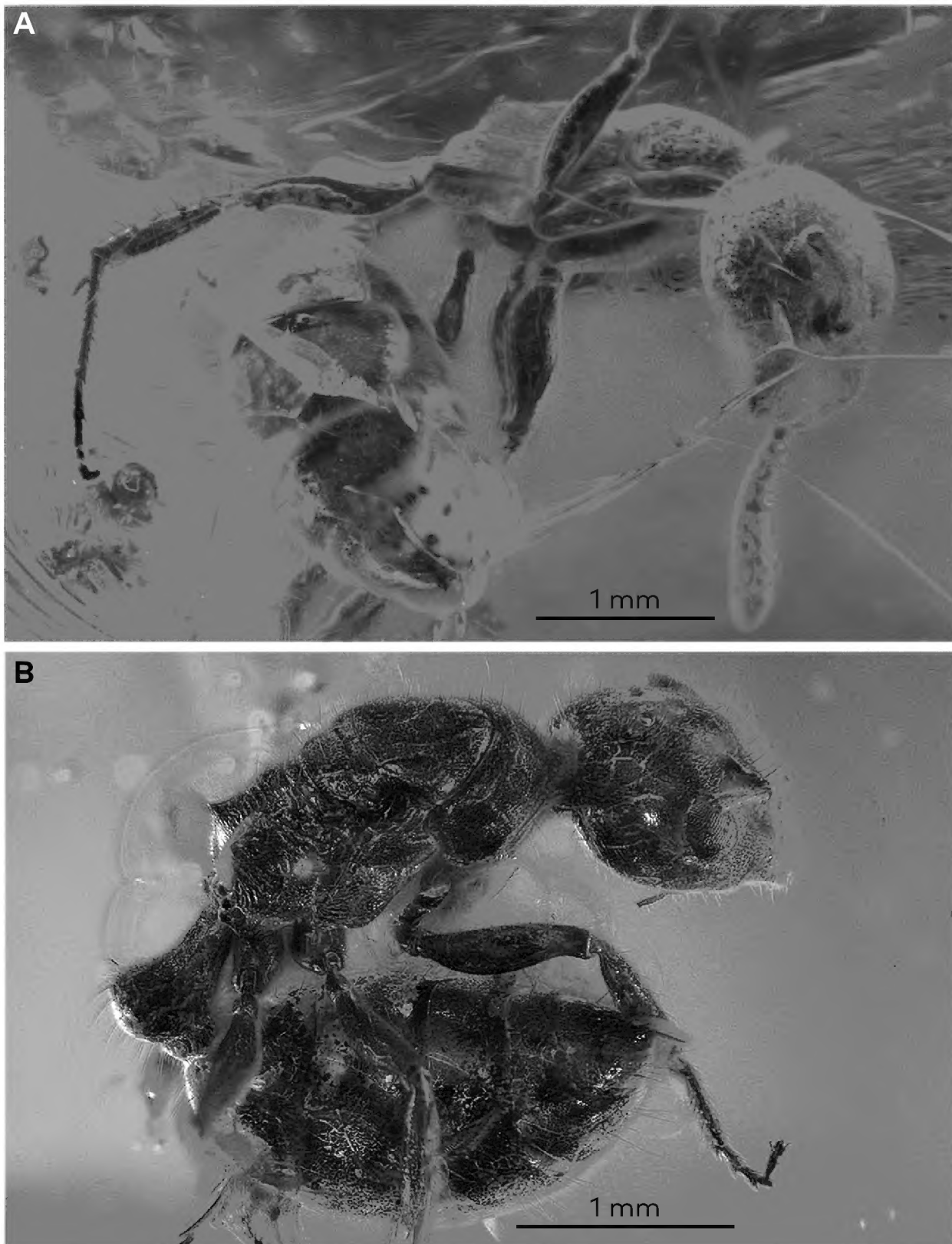


Figure 1. Photograph of *Protaneuretus succineus* Wheeler, 1915; **A** worker (collection number F-200, Rovno amber), body in lateral view; **B** queen (Baltic amber), body in lateral view (A photo A. Radchenko; B photo from archive of G.M. Dlussky).

Wheeler (1915) established *Protaneuretus* and *Paraneuretus* based on specimens from late Eocene Baltic amber (Priabonian, 37.8–33.9 Ma). Wheeler (1915) described *Protaneuretus succineus* from four workers and one queen. Ours is the first published record of *P. succineus* in the 100+ years since its description. Recently, a second member of the genus, *Protaneuretus mirabilis* Dubovikoff et Dlussky, 2020, was described from the contemporaneous Bitterfeldian amber (Germany) (Dubovikoff et al. 2020). Wheeler (1915) described two species of *Paraneuretus*: *P. tornquisti* based on 22 workers and two males, and *Protaneuretus longicornis* Wheeler, 1915, based on a single male. Dlussky and Rasnitsyn (2009) found six more workers of *P. tornquisti* in Baltic amber and first recorded it from Bitterfeldian amber. Dlussky et al. (2015) described a third species in the genus, *Paraneuretus dubovikoffi*, based on the imprints of worker and queen from the Russian Far East (latest Eocene). The differences between workers of *P. succineus* and *P. tornquisti* are explained in Table 1.

A third genus and species of Aneuretinae from late Eocene European ambers, *Pityomyrmex tornquisti* Wheeler, 1915, is known only from the holotype specimen, and differs from both of the above aneuretine genera by having very long, falcate mandibles, equipped with small numerous subequal denticles on the inner margin (see Wheeler 1915, fig. 48).

Wheeler (1915) did not indicate the number of maxillary and labial palps in *Protaneuretus succineus*. Despite the fact that the ventral part of the head of the specimen we studied is partially covered with a white film, the maxillary palps appear to be 6-segmented and extend far beyond the midlength from their base to the occipital foramen, and the labial palps are 4-segmented.

Below are the measurements (in mm) and indices of various morphological features of the studied specimens:

Protaneuretus succineus – total length 6.3, HL 1.32, SL 0.94, OL-1 0.31, OL-2 0.29, MsL 0.34, MdL 0.60, ML 1.90, MH 0.57, PL 0.73, PH 0.57, HTL 1.01, HFL 1.07, fun1L 0.12, fun2L 0.12; indices: SI 0.71, OI-1 0.24, OI-2 1.09, MsI 1.08, MdI 0.45, PI-1 1.27, PI-2 0.55, MI 3.32, funI 1.00.

Paraneuretus tornquisti – total length 8.6, HL 1.85, SL 2.13, OL-1 0.46, OL-2 0.42, MsL 0.52, MdL 0.78, ML 3.07, MH 0.94, PL 0.75, PH 0.68, HTL 2.29, HFL 2.47, fun1L 0.29, fun2L 0.36; indices: SI 1.09, OI-1 0.21, OI-2 1.09, MsI 1.14, MdI 0.40, PI-1 1.12, PI-2 0.39, MI 3.28, funI 1.27.

Our present study increases the number of published ant records in this amber to 77 species from 39 genera and 9 subfamilies. We have found about 45 additional new or previously unrecorded ant taxa from this amber, which we will consider in future publications (our unpublished data).

Discussion

Our records of *Protaneuretus succineus* and *Paraneuretus tornquisti* in Rovno amber indicate that in the late Eocene Aneuretinae were distributed both on the northern

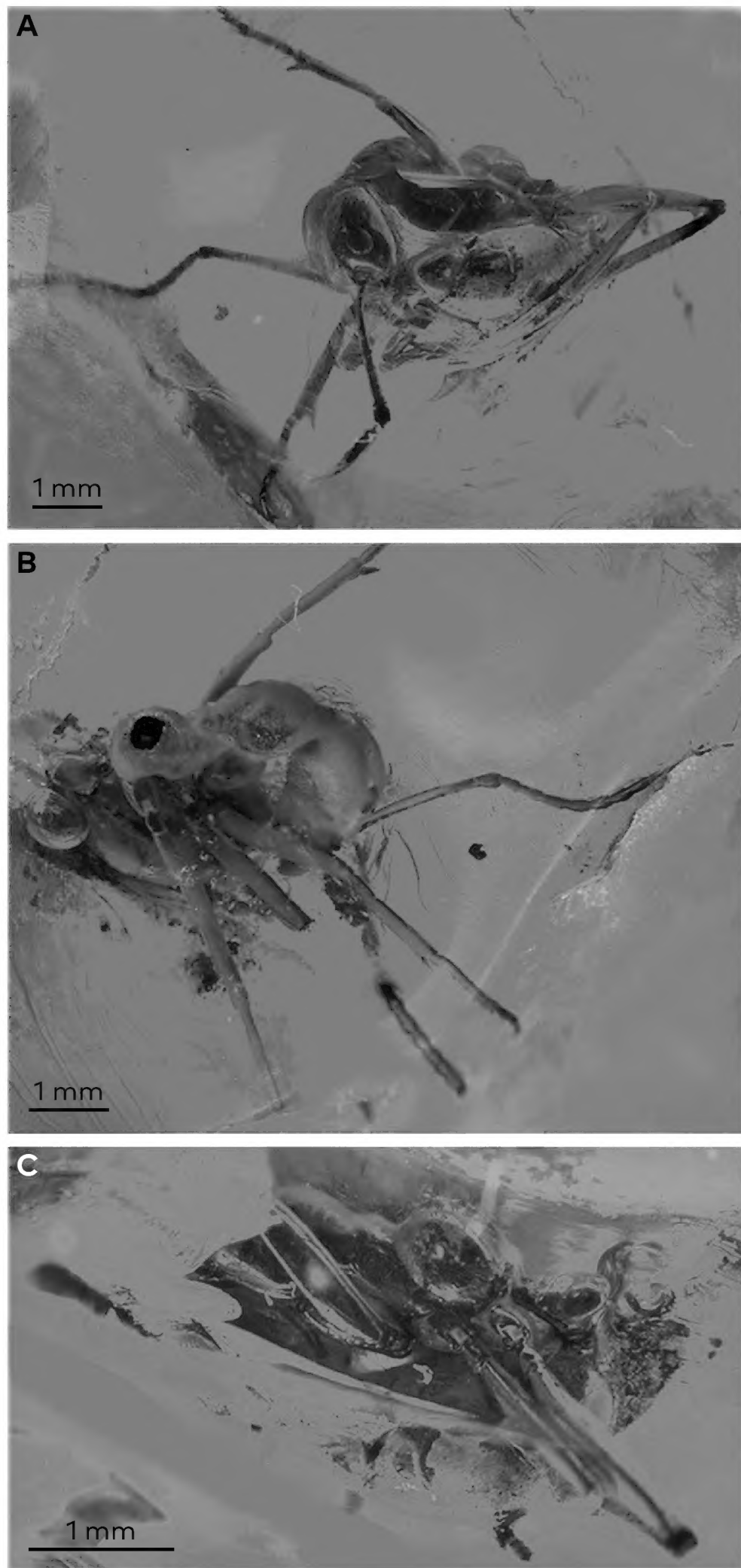


Figure 2. Photograph of *Paraneuretus tornquisti* Wheeler, 1915, worker (collection number K-9135, Rovno amber); **A** body in left lateral view; **B** body in right lateral view; **C** mesosoma and abdomen in left lateral view (photo A. Radchenko).

Table 1. Differences between workers of *P. succineus* and *P. tornquisti*- include the following (based on Wheeler 1915, with our additions):

<i>Protaneuretus succineus</i>	<i>Paraneuretus tornquisti</i> -
Propodeum slightly convex, with two short sharp teeth, directed upward	Propodeum inflated and gradually rounded, without teeth
Antennal scape shorter than head (SL < HL)	Antennal scape longer than head (SL > HL)
Entire body, including scapes and legs, with abundant long erect hairs	Head and mesosoma with sparse erect hairs; all gastral sternites and tergites, starting from third, with abundant long erect hairs; petiole, scapes and legs (except coxae) without hairs
Mesopleurae and sides of propodeum with longitudinal rugae, propodeal dorsum with transverse rugosity	Entire body smooth
Helcium attached on the middle of anterior face of first gastral segment	Helcium attached high on anterior face of first gastral segment

and southern coasts of the Paratethys. Paleontological evidence indicates that Aneuretinae were widely distributed only in the Northern Hemisphere in areas lying approximately between 40°–55° N and 105° W–143° E, starting from the Cretaceous to the late Eocene. Interestingly, none of the fossil Aneuretinae genera are known to have survived beyond the late Eocene. Most likely, this was due to the Eocene-Oligocene climatic shift, when the mean annual temperature dropped abruptly by several degrees (Westerhold et al. 2020). The so called “equable” Eocene climate at high latitudes with reduced thermal seasonality and higher mean temperature of the cold months and milder winters was replaced by a colder one with pronounced seasonality. Such climatic conditions had allowed organisms that now inhabit either temperate or tropical and subtropical regions to live in the same habitats (“Wheeler’s dilemma”) (Archibald and Farrell 2003; Radchenko and Perkovsky 2021).

Ward et al. (2010) concluded that Aneuretinae is a sister group to all Dolichoderinae, and the origin of crown dolichoderomorphs (Dolichoderinae + Aneuretinae) occurred about 98 Ma (CI = 82–114). Aneuretinae could be thought of Dolichoderinae with a sting, though this important feature is visible only in two fossil genera preserved in amber, *Protaneuretus* and *Paraneuretus*. In addition, the presence of a well-developed and functional sting is plesiomorphic, i.e., the apomorphic character state is the reduced sting in Formicinae and Dolichoderinae. Elucidation of the correct taxonomic position of many fossil genera assigned to this subfamily requires additional material and further studies.

The proposed morphological diagnosis of Aneuretinae (Wilson et al. 1956; Bolton 2003) is based primarily on workers and queens of extant *Aneuretus simoni* and includes only two autapomorphies compared to Formicinae and Dolichoderinae: a) petiole with a long anterior peduncle; b) helcium is attached high on the anterior face of the first gastral segment (abdominal segment III). The location of the helcium, however, is high only in some fossil Aneuretinae species, e.g. *P. tornquisti*,

P. dubovikoffi Dlussky, Rasnitsyn et Perfilieva, 2015 (Russian Far East, late Eocene, ~35–34 Ma), *Cananeuretus occidentalis* Engel et Grimaldi, 2005 (Canada, Cretaceous, Campanian, 83.6–71.2 Ma) and probably in *Pityomyrmex tornquisti* and *Aneuretellus deformis* Dlussky, 1988 (Sahkalinian amber, middle Eocene, 47–43 Ma), but it attaches to the middle of the anterior face of the first gastral segment (or even somewhat lower) in *Protaneuretus succineus*, *P. mirabilis*, and probably in *Napakimyrmex paskapooensis* LaPolla et Barden, 2018 (Canada, Alberta, Paleocene, 60.2–56.0 Ma).

Boudinot (2015) and LaPolla and Barden (2018) have expressed doubts about the assignment of several fossil genera to Aneuretinae, including *Pityomyrmex tornquisti*. However, based on the Wheeler's (1915) original description and drawing, we agree with its transfer from Dolichoderinae to Aneuretinae. Wheeler (loc. cit.: 99, fig. 48) wrote: "Petiole much longer than broad, pedunculate in front, with a small node near its posterior end... thorax and petiole recall these parts in *Paraneuretus*". The sting is not visible on the holotype specimen due to its position in the amber, but the helcium appears to be attached high to the anterior face of the first gastral segment. None of the known extant and extinct Dolichoderinae and Formicinae genera have a similarly shaped petiole. On the other hand, the meso- and metatibiae of *Pityomyrmex* worker have two spurs, pectinate and simple, and very peculiar mandibles, which are also unknown in Dolichoderinae and Formicinae. In any case, additional material is needed to definitely determine the taxonomic position of *Pityomyrmex*, but among all modern or extinct ant subfamilies, it fits Aneuretinae rather than any other.

The gyne of *Dolichoderus anglicus* Cockerell, 1915 (United Kingdom, Isle of Wight, late Eocene, Priabonian) can be assigned to Dolichoderinae or Aneuretinae based on the venation of the forewing. Dlussky and Perfilieva (2014) established for it a new genus *Britaneuretus* based on the shape of propodeum and transferred it to the subfamily Aneuretinae. They also noted that *Britaneuretus* differs from several other fossil aneuretine genera, including *Minaeuretus* Carpenter, 1930, by the absence of a petiolar node. However, in the photograph of the holotype of *B. anglicus* (loc. cit., plate 18, fig. 1), the petiole has a distinct peduncle and a not high, but distinct node. At the same time, wingless queens of *Minaeuretus mirabilis* Carpenter, 1930 (USA, Florissant, late Eocene, Priabonian) and *M. eocenicus* Dlussky et Rasnitsyn, 2003 (misspelled as *Mianeuretus*) (USA, Green River, early Eocene, Ypresian, 53.5–48.5 Ma; see Smith et al. 2008) morphologically almost indistinguishable from *Britaneuretus*. On the other hand, given the shape of the petiole and propodeum, both *Britaneuretus* and *Minaeuretus* belong rather to Aneuretinae (or to the still unknown Dolichoderinae lineage, which is much less likely), but not to *Dolichoderus* Lund, 1831 or other dolichoderines. However, their assignment to Aneuretinae remains uncertain.

The broad distribution of fossil representatives of the crown-group Dolichoderinae and Aneuretinae in North America and Eurasia suggests that they originated in the Northern Hemisphere. A Northern Hemisphere origin for Aneuretinae may seem surprising given the distribution of modern *A. simoni* in Sri Lanka. However, Sri Lanka as a part of the Indian subcontinent, which drifted away from the ancient supercontinent Gondwana and collided with Asia in the early Eocene (Ypresian,

~55–50 Ma) (Zhu et al. 2005; Wang et al. 2008), and early Eocene Cambay amber (India, Ypresian, ~52–50 Ma) contains yet undescribed ants tentatively assigned to several subfamilies, including Aneuretinae (Rust et al. 2010; Barden 2017). It seems likely that aneuretine ants entered India (and then Sri Lanka) after its connection with Asia.

The mystery remains as to why *A. simoni* is the only Aneuretinae to survive to the present day, and why it survived only in Sri Lanka. Compared to fossil *Protaneuretus* and *Paraneuretus*, the extant *A. simoni* has several specialized morphological features, notably an extremely elongated petiole and a reduced number of maxillary palps (from six in the two fossil genera to three in *A. simoni*). In addition, workers of *A. simoni* are dimorphic, which is likely an evolutionarily advanced trait. Wilson et al. (1956) seeking to explain why *A. simoni* survived in Sri Lanka not in neighboring areas, suggested that this species is not a natural dweller of primary rainforests, but inhabits relatively dry, more open forests and clearings. They supposed that such environmental conditions are favorable for *A. simoni* due to the relatively low abundance of its main ant competitors, species of the genera *Pheidole* Westwood, 1839 and *Crematogaster* Lund, 1831. More research is needed to understand the 34-million-year age gap between the youngest Aneuretinae fossils and the single relict Aneuretinae species, *A. simoni*.

Acknowledgements

We are genuinely grateful to Dr. J. K. Wetterer (USA) for very valuable advice on improving the manuscript and for correcting the English; we also grateful to Dr. E. E. Perkovsky (Ukraine) for providing the specimen (K-9135) for the investigation. This work was supported by the grant NRFU (Ukraine) No. 2020/02/0369 (to A. Radchenko).

References

- Archibald SB, Farrell BD (2003) Wheeler's dilemma. *Acta Zoologica Cracoviensia* 46 (Supplement Fossil Insects): 17–23.
- Barden P (2017) Fossil ants (Hymenoptera: Formicidae): ancient diversity and the rise of modern lineages. *Myrmecological News* 24: 1–30. https://doi.org/10.25849/myrmecol.news_024:001
- Bolton B (2003) Synopsis and classification of Formicidae. *Memoirs of the American entomological Institute* 71: 1–370.
- Boudinot BE (2015) Contributions to the knowledge of Formicidae (Hymenoptera, Aculeata): a new diagnosis of the family, the first global male-based key to subfamilies, and a treatment of early branching lineages. *European Journal of Taxonomy* 120: 1–62. <http://dx.doi.org/10.5852/ejt.2015.120>

- Boudinot BE, Khouri Z, Richter A, Griebenow ZH, van de Kamp T, Perrichot V, Barden Ph (2022) Evolution and systematics of the Aculeata and kin (Hymenoptera), with emphasis on the ants (Formicoidea: †@@@idae fam. nov., Formicidae). bioRxiv preprint: 1–359. <https://doi.org/10.1101/2022.02.20.480183>
- Carpenter FM (1930) The fossil ants of North America. Bulletin of the Museum of Comparative Zoology 70: 1–66. https://www.antwiki.org/wiki/images/7/73/Carpenter_1930.pdf
- Clark J (1951) The Formicidae of Australia. Vol. 1. Subfamily Myrmeciinae. CSIRO, Melbourne, 230 pp. https://www.antwiki.org/wiki/images/e/e5/Clark_1951.pdf
- Cockerell TDA (1915) British fossil insects. Proceedings of the United States National Museum 49: 469–499. https://www.antwiki.org/wiki/images/7/76/Cockerell_1915.pdf
- Dlussky GM (1988) Murav'i Sahalinskogo yantarya (Paleotsen?). Paleontologicheskii Zhurnal No. 1: 50–61. [in Russian] https://www.antwiki.org/wiki/images/6/61/Dlussky_1988aSakhalin_amber.pdf
- Dlussky GM (1996) Murav'i (Hymenoptera: Formicidae) Birmanskogo yantarya. Paleontologicheskii Zhurnal, No. 3: 83–89. [in Russian]
- Dlussky GM, Perfilieva KS (2014) Superfamily Formicoidea Latreille, 1802. In: Antropov AV, Belokobylskij SA, Compton SG, Dlussky GM (Eds) The wasps, bees and ants from the Insect Limestone (Late Eocene) of the Isle of Wight, U.K. Earth and Environmental Science. Transactions of the Royal Society of Edinburgh 104: 410–438. <https://doi.org/10.1017/S1755691014000103>
- Dlussky GM, Rasnitsyn AP (2003). Ants (Hymenoptera: Formicidae) of formation Green River and some other Middle Eocene deposits of North America. Russian Entomological Journal 11: 411–436. https://www.antwiki.org/wiki/images/f/fc/Dlussky_%26_Rasnitsyn_2003.pdf
- Dlussky GM, Rasnitsyn AP (2009) Ants (Insecta: Vespida: Formicidae) in the Upper Eocene amber of Central and Eastern Europe. Paleontological Journal 43: 1024–1042. <https://doi.org/10.1134/S0031030109090056>
- Dlussky GM, Rasnitsyn AP, Perfilieva KS (2015) The Ants (Hymenoptera: Formicidae) of Bol'shaya Svetlovodnaya (Late Eocene of Sikhote-Alin, Russian Far East). Caucasian entomological bulletin 11: 131–152. <https://doi.org/10.23885/1814-3326-2015-11-1-131-152>
- Dubovikoff DA, Dlussky GM, Perkovsky EE, Abakumov EV (2020) A new species of the genus *Protaneuretus* Wheeler (Hymenoptera, Formicidae) from Bitterfeld amber (late Eocene) with species key of the genus. Paleontological Journal 54: 389–391. <https://doi.org/10.1134/S003103012004005X>
- Emery C (1913) Hymenoptera, Fam. Formicidae, subfam. Dolichoderinae. In: Wytsman P (Ed.) Genera Insectorum. Fasc. 137 (1912). Bruxelles, 50 pp.
- Engel MS, Grimaldi DA (2005) Primitive new ants in Cretaceous amber from Myanmar, New Jersey and Canada. American Museum Novitates 3485: 1–23. https://www.antwiki.org/wiki/images/a/a9/Engel_%26_Grimaldi_2005.pdf
- LaPolla JS, Barden P (2018) A new aneuretine ant from the Paleocene Paskapoo Formation of Canada. Acta Palaeontologica Polonica 63: 435–440. <https://doi.org/10.4202/app.00478.2018>

- Lucena DAA, Melo GAR (2018) Chrysidid wasps (Hymenoptera: Chrysididae) from Cretaceous Burmese amber: phylogenetic affinities and classification. *Cretaceous Research* 89: 279–291. <https://doi.org/10.1016/j.cretres.2018.03.018>
- Perkovsky EE (2016) Tropical and Holarctic ants in Late Eocene ambers. *Vestnik zoologii* 50: 111–122. <https://doi.org/10.1515/vzoo-2016-0014>
- Radchenko A (2020) New species of extinct ant genus *Eocenomyrma* Dlussky et Radchenko (Hymenoptera: Formicidae: Myrmicinae) from the Baltic amber. *Annales Zoologici* 70: 109–111. <https://doi.org/10.3161/00034541ANZ2020.70.1.005>
- Radchenko A (2021) New species of the fossil ant genus *Drymomymex* (Hymenoptera, Formicidae, Formicinae) from the late Eocene Rovno amber (Ukraine). *Palaeoentomology* 4: 544–549. <https://doi.org/10.11646/palaeoentomology.4.6.4>
- Radchenko AG, Dlussky GM (2016) Further data on the extinct ant genus *Eocenomyrma* (Hymenoptera, Formicidae). *Vestnik zoologii* 50: 395–406. <https://doi.org/10.1515/vzoo-2016-0046>
- Radchenko AG, Dlussky GM (2018a) Ants of the genus *Fallomyrma* Dlussky et Radchenko (Hymenoptera, Formicidae, Myrmicinae) from Late Eocene European Ambers. *Paleontological Journal* 52: 155–163. <https://doi.org/10.1134/S0031030118020107>
- Radchenko A, Dlussky GM (2018b) Two new fossil species of the ant genus *Pristomyrmex* Mayr (Hymenoptera, Formicidae) from the Rovno and Bitterfeld ambers. *Annales Zoologici* 68: 251–258. <https://doi.org/10.3161/00034541ANZ2018.68.2.004>
- Radchenko A, Dlussky GM (2019) The first record of the ant genus *Crematogaster* (Hymenoptera, Formicidae) from the late Eocene European amber. *Annales Zoologici* 69: 417–421. <https://doi.org/10.3161/00034541ANZ2019.69.2.008>
- Radchenko A, Dlussky GM, Perfilieva KS (2018) A new extinct ant genus (Hymenoptera, Formicidae, Myrmicinae) from the Late Eocene Rovno amber – a putative ancestor of the *Leptothorax* genus group. *Myrmecological News* 27: 111–117. https://doi.org/10.25849/myrmecol.news_027:111
- Radchenko AG, Khomych MR (2020) Ants of the extinct genus *Cataglyphoides* Dlussky (Hymenoptera: Formicidae: Formicinae) from the late Eocene European ambers. *Invertebrate Zoology* 17: 154–161. <https://doi.org/10.15298/invertzool.17.2.05>
- Radchenko AG, Perkovsky EE (2018). First record of fossil ant species *Eocenomyrma rugosostriata* (Mayr) (Hymenoptera: Formicidae) from the Rovno amber. *Russian Entomological Journal* 27: 285–288. <https://doi.org/10.15298/rusentj.27.3.08>
- Radchenko AG, Perkovsky EE (2020) New finds of the fossil ant genus *Prionomyrmex* Mayr (Hymenoptera, Formicidae, Myrmecinae) in Late Eocene European Ambers. *Paleontological Journal* 54: 617–626. <https://doi.org/10.1134/S0031030120060088>
- Radchenko AG, Perkovsky EE (2021) Wheeler's dilemma revisited: first *Oecophylla-Lasius* syninclusion and other ants syninclusions in the Bitterfeld amber (late Eocene). *Invertebrate Zoology* 18: 47–65. <https://doi.org/10.15298/invert-zool.18.1.05>
- Radchenko AG, Perkovsky EE, Vasilenko DV (2021) *Formica* species (Hymenoptera, Formicidae, Formicinae) in late Eocene Rovno amber. *Journal of Hymenoptera Research* 82: 237–251. <https://doi.org/10.3897/jhr.82.64599>

- Radchenko AG, Proshchalykin MYu (2021) New extinct ant genus (Hymenoptera, Formicidae, Myrmicinae) from late Eocene Rovno amber. In: Proshchalykin M, Gokhman V (Eds) Hymenoptera studies through space and time: A collection of papers dedicated to the 75-th anniversary of Arkady S. Lelej. *Journal of Hymenoptera Research* 84: 271–282. <https://doi.org/10.3897/jhr.84.65238>
- Rust J, Singh H, Rana RS, McCann T, Singh L, Anderson K, Sarkar N, Nascimbene PC, Stebner F, Thomas JC, Solórzano Kraemer M, Williams ChJ, Engel MS, Sahni A, Grimaldi D (2010) Biogeographic and evolutionary implications of a diverse paleobiota in amber from the early Eocene of India. *Proceedings of the National Academy of Sciences of the United States of America* 107: 18360–18365. www.pnas.org/cgi/doi/10.1073/pnas.1007407107
- Smith ME, Carroll AR, Singer BS (2008) Synoptic reconstruction of a major ancient lake system: Eocene Green River Formation, western United States. *Geological Society of America Bulletin* 120: 54–84. <https://doi.org/10.1130/B26073.1>
- Wang Ch, Zhao X, Liu Zh, Lippert PC, Graham SA, Coe RS, Yi H, Zhu L, Kiu S, Li Y (2008) Constraints on the early uplift history of the Tibetan Plateau. *Proceedings of the National Academy of Sciences of the United States of America* 105: 4987–4992. www.pnas.org/cgi/doi/10.1073/pnas.0703595105
- Ward P, Brady SA, Fisher B, Schultz TR (2010) Phylogeny and biogeography of Dolichoderine ants: effects of data partitioning and relict taxa on historical inference. *Systematic Biology* 59: 342–362. <https://doi.org/10.1093/sysbio/syq012>
- Westerhold T, Marwan N, Drury AJ, Diederik Liebrand D, Agnini C, Anagnostou E, Barnett JSK, Bohaty SM, De Vleeschouwer D, Florindo F, Frederichs T, Hodell DA, Holbourn AE, Kroon D, Lauretano V, Littler K, Lourens LJ, Lyle M, Pälike H, Röhl U, Tian J, Wilkens RH, Wilson PA, Zachos JC (2020) An astronomically dated record of Earth's climate and its predictability over the last 66 million years. *Science* 369: 1383–1387. <https://doi.org/10.1126/science.aba6853>
- Wheeler WM (1915) The ants of the Baltic Amber. *Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg in Preußen* 55: 1–142. https://www.antwiki.org/wiki/images/ec/Wheeler_1915i.pdf
- Wilson EO, Eisner T, Wheeler GC, Wheeler J (1956) *Aneuretus simoni* Emery, a major link in ant evolution. *Bulletin of the Museum of Comparative Zoology at Harvard College* 115: 81–99. https://www.antwiki.org/wiki/images/c/c4/Wilson_et_al_1956.pdf
- Zhu B, Kidd WSE, Rowley DB, Currie BS, Shafique N (2005) Age of initiation of the India-Asia collision in the East-Central Himalaya. *The Journal of Geology* 113: 265–285.